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# Land use and population growth of *Primula veris*: an experimental demographic approach

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## Summary

**1.** Changes in land use are the primary cause of decline for many plant species. Efficient management actions for such species must be based on knowledge of the key phases of the plant life cycles that respond most to changes in environmental factors.
**2.** To assess how grazing influences population viability of the perennial rosette herb *Primula veris*, we applied four experimental treatments to abandoned grasslands and recorded the demographic response in permanent plots and seed sowing experiments over 3 years.
**3.** Treatments had strong effects on population viability. Transition matrix models showed that cutting the surrounding vegetation had no effect on population growth rate (λ). However, when this was combined with litter removal λ increased to 1·46, compared with 1·11 in controls. With disturbance and complete removal of the surrounding vegetation the effect was even stronger, and λ increased to 1·60.
**4.** Increases in λ were primarily a result of increased growth of the smallest rosettes, and increased seedling production. In contrast, the performance of larger *P. veris* individuals was not affected by experimental treatments.
**5.** The higher the elasticity of a particular life cycle transition, the less the change in the transition rate caused by treatments. This suggests that plants are able partly to buffer the effects of environmental variation by minimizing changes in the life cycle transitions that are most important to population growth rate.
**6.** *Synthesis and applications*. Experimental demographic approaches provide an important tool for assessing how grazing and other types of management influence species viability, and help to unravel the mechanisms underlying such relationships. With such information it is possible to predict the effects of novel types of management and land-use scenarios on population viability. For *P. veris*, we identified seedling establishment as a key phase in the life cycle, and litter accumulation as a key environmental factor, suggesting that these should be prime targets for management. One practice that is likely to favour as well as seedling establishment preventing litter accumulation is late summer grazing.

*Key-words*: disturbance, grazing, litter, matrix models, seedling recruitment

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## Introduction

Many plant species depend on continuous management, in terms of grazing or mowing, for their survival in the agricultural landscape. Changes in land-use practices may result in continuously or more abruptly deteriorating environmental conditions for these species. For species conservation, one of the most important tasks is therefore to assess the effects of changes in land use on population viability (Burgman, Akcakaya & Loew 1998; Brussard 1991; Horvitz & Schemske 1995). Two important steps in such assessments are to relate

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population viability to the underlying demographic processes, and variation in demographic processes to environmental differences (Norris 2004).

Population viability can, in principle, be linked to environmental variation by examining demographic information from a range of habitats. Many recent studies have demonstrated considerable spatiotemporal variation in vital rates, but there is still relatively little information about how such variation is correlated with abiotic and biotic environmental factors (but see Bullock, Hill & Silvertown 1994; Canales *et al*. 1994; Oostermeijer *et al*. 1996; Lesica 1999; Lennartsson & Oostermeijer 2001). From a conservation point of view, it is essential to have not only a phenomenological understanding of the relationship between habitat quality and species performance, but also an explicit knowledge of the specific environmental factors underlying such relationships.

Grazing is likely to affect plant performance in many ways, such as through changes in competition for light, litter accumulation, disturbance frequency and direct damage of plants. Moreover, the intensity of grazing is likely to be correlated with habitat characteristics, such as topography, soil chemistry and humidity. Correlations between grazing and plant performance therefore cannot pinpoint the mechanisms that are important and do not prove causation. To assess the overall effects of grazing, and the relative importance of the different processes associated with it, we need to carry out experimental manipulations in natural systems. Ideally, manipulations should be both replicated and carried out in a fashion that ensures that effects during the entire life cycle can be assessed.

Estimating the net effects of environmental factors, such as grazing, on plant performance constitutes a particular challenge in iteroparous plants, because life cycles are complex and life spans often considerably exceed the life span of experiments. Variation in components of plant fitness, for example seed production, growth and survival to maturity, often provide poor estimates of the total effects of environmental variation (Ehrlén 2003). The growth rate of a population can be regarded as an omnibus index of the cumulative contributions of the underlying demographic processes, and thus constitutes a much more complete demographic estimate of effects. Detailed demographic studies in combination with experimental manipulations of the environment therefore offer a powerful means of assessing the total effects, in terms of population growth rate, and partitioning effects into contributions from each of the vital rates (Caswell 1989, 2001; Horvitz, Schemske & Caswell 1997). The latter is important because it enables us to identify key phases of the life cycle that are responsible for differences in population viability, and to direct management efforts in an optimal way. Notwithstanding the advantages, relatively few studies have combined manipulations of the environment with demographic studies over several years (but see Bullock, Hill & Silvertown 1994; Canales *et al*. 1994; Lesica 1999; Lennartsson & Oostermeijer 2001).

In this study we examined how different environmental factors associated with grazing influenced the demography of the perennial herb *Primula veris* L. (Primulaceae). We experimentally manipulated three main components of the environment: competition for light, litter accumulation and disturbance frequency. We addressed two main questions. (i) What are the effects of treatments on fitness components, such as seedling establishment and seedling survival, and survival, growth, flowering and seed production of established individuals? (ii) What are the total effects of treatments on population performance, in terms of growth rate? A demographic modelling approach based on transition matrices was used to calculate the total effects on population growth rate. These models also enabled decomposition of the total treatment effects into contributions from changes in each of the life-cycle transitions.

## Materials and methods

### THE SPECIES

The study species *P. veris* is a rosette-forming hemicryptophytic perennial herb. Individual plants may live for several decades (Inghe & Tamm 1988). Large rosettes sometimes split into two (Tamm 1972). *Primula veris* has one or a few inflorescences that emerge in spring. Each stalk usually has five to 10 flowers, which open synchronously in May. Flowering continues for 2–3 weeks and the seeds ripen in late July and August. Seeds are relatively small (mass, mg, mean ± SE, 0·86 ± 0·044, $n = 66$ plants). It has been suggested that *P. veris* only has a transient seed bank (Thompson, Bakker & Bekker 1997). However, in our study area we have evidence that the species possesses a permanent seed bank (K. Lehtilä, R. Leimu, K. Syrjänen, M. B. Garcia & J. Ehrlén, unpublished data). *Primula veris* is an obligate outbreeder (Wedderburn & Richards 1990) and the flowers are distylic. Seed predation is common in some populations (Leimu *et al*. 2002). The main seed predators of *P. veris* in the study area are larvae of the plume moth *Amblyptilia punctidactyla* (Pterophoridae).

The main distribution area of *P. veris* is the temperate zone of central and eastern Europe (Hultén 1971; Hultén & Fries 1986). Historically, occurrence in the northern part of the distribution area is closely linked with grazing and mowing, although the latter almost disappeared from the area during the last century. However, the species is capable of persisting at many sites several decades after management has ceased (J. Ehrlén, unpublished data).

### EXPERIMENTAL DESIGN

The data for this study were collected in a 1 × 1-km area situated near Tullgarn, about 60 km south of Stockholm, south-east Sweden. The demography of five unmanipulated populations within the study area was followed simultaneously (K. Lehtilä, R. Leimu, K. Syrjänen, M. B. Garcia & J. Ehrlén, unpublished data). In May 1996

we selected six sites within the area for experimental manipulation. We selected sites where the previous mowing or grazing management of the field layer had been abandoned, but where the bush and tree canopy was very sparse. At each site four 2 × 2-m plots were established. Each plot was assigned at random to one of four experimental treatments. The experimental treatments were: (i) control, (ii) vegetation removal, (iii) litter removal plus vegetation removal, and (iv) soil disturbance plus vegetation removal. Treatments were designed to mimic the components of management that we predicted were important to the performance of *P. veris* individuals, rather than corresponding with actual management scenarios. Within each plot the locations of all individuals were mapped.

### TREATMENT APPLICATIONS

The application of the experimental treatments was initiated after recording the state of the plants in June 1996, and the last treatment was applied in June 1998. Plots received the same treatment during the entire period. For the vegetation removal treatment, the surrounding vegetation was cut to approximately 2 cm in height at the peak of flowering in June 1996 and 1997, leaving *P. veris* individuals intact. The litter removal treatment was carried out by raking at the onset of vegetative growth in early May 1997 and 1998. The soil disturbance treatment plus vegetation removal was carried out at the peak of flowering and was achieved by removing all above-ground parts and as much as possible of below-ground parts, again leaving *P. veris* individuals intact. Because of the removal of below-ground parts this treatment also implied a remixing of the upper soil layer.

### PLANT PARAMETERS

Each individual was recorded twice each year, and followed from 1996 to 1998. In June, the number of leaves, length of the largest leaf and proportion of leaf area removed by herbivores was recorded for each plant, and flower number was counted in all fertile individuals. In August the numbers of intact and damaged capsules were counted. At each visit emerged seedlings were searched for, recorded and included in the further study. Vegetation removal and soil disturbance were applied to plots for the first time in June 1996, after the recording of vegetative characters, flowering state, flower number and leaf damage. Litter removal was first carried out in early May 1997. Hence, characteristics recorded in June 1996 were not affected by any treatments, whereas fruit set and capsule predation, recorded in August 1996, were potentially affected by vegetation removal or soil disturbance treatments the same year.

### RECRUITMENT EXPERIMENTS

The effect of treatments on seedling emergence and seedling survival was examined by seed-sowing experiments. For these experiments, the environmental treatments were carried out as in the main experiment. In 1996 four plots, 10 × 10 cm, per site and treatment (total $n = 96$) were established and randomly assigned to one of four seed densities: (i) no seeds, only natural seed rain, (ii) 50 seeds, (iii) 200 seeds and (iv) 500 seeds sown. The seeds added produced an increase in seed density corresponding to 5000–50 000 $m^{-2}$. The sowing densities were several orders of magnitude higher than the natural seed rain (mean ± SD, 13·5 ± 13·2 seeds per $dm^2$, $n = 6$ permanent plots). In 1997 a further seed-sowing experiment was performed using only the 50 seeds $plot^{-1}$ density. Seeds for the sowing experiments were collected in the immediate neighbourhood of each plot at the time of fruit maturation and originated from a sample of several seed parents. Seeds were examined for predation and intact seeds were sown within 24 h of collection. All plots were censused at least once every month during May–July from 1996 to 1998.

### DATA ANALYSIS

Because the treatments were applied plotwise, the contrast between individuals in plots exposed to the different treatments had to use plots as replicates and examine variance in plot means. Differences in survival were examined by two-way ANCOVA, with treatment and site as the main factors and leaf length in 1996 as the covariate. Differences in leaf number, size of the largest leaf, probability of flowering, flower number and leaf damage were examined by repeated-measurement ANCOVA, with plot averages in 1997 and 1998 as dependent variables, treatment and site as the main factors and initial average size (1996) as the covariate. Differences in fruit set and capsule predation were examined by repeated-measurement ANOVA, with plot averages 1996, 1997 and 1998 as dependent variables, and treatment and site as the main factors. The effects of seed-sowing densities and treatments on the proportion of seeds that emerged as seedlings the year after sowing, seedling number the second year after sowing, and seedling size 2 years after sowing, were examined by two-way ANOVAS. The treatments were not replicated within sites and the interaction effect treatment × site could thus not be separated from the error term.

All proportions were arcsine square root-transformed before statistical analysis. Means presented are back-transformed values. In tests of differences in size, only surviving individuals with above-ground parts were included. Differences in the proportion of individuals flowering were investigated for individuals with a largest leaf length of more than 40 mm because smaller individuals never flowered. Analyses of flowering frequency based on all non-seedling individuals yielded similar results (data not presented).

The total fitness effects of different treatments were estimated by changes in population growth rate ($\lambda$). Population growth rates for each treatment category were calculated by transition matrix models of the form

$\mathbf{n}(t+1) = \mathbf{An}(t)$ (Caswell 2001). The matrix **A** describes how individuals of each stage class in the vector $\mathbf{n}(t)$ contribute to the stage classes in $\mathbf{n}(t+1)$. **A** yields information on stable stage distribution and population growth rate. To build a matrix model of the dynamics of populations consisting of different treatment groups, *P. veris* individuals were assigned to one of six stages: (i) seeds, in the seed bank; (ii) seedlings; (iii) small, individuals 2 or more years old but in the seedling size range (length of largest leaf = 17 mm); (iv) intermediate, individuals larger than seedlings but smaller than the minimum size at which reproduction occurs (18–40 mm); (v) large, vegetative individuals above the minimal size of reproduction (41 mm) but not flowering; (vi) reproductive, flowering individuals. The numbers of intact and damaged capsules were counted in individuals in permanent plots but the number of intact seeds per fruit was estimated from capsules collected outside plots. Germination rates and survival in the soil seed bank were estimated from the seed-sowing experiments. Germination probability was calculated as the number of seedlings emerging in sowing plots minus the number of seedlings emerging in unsown control plots, divided by the number of seeds sown. We used plots with 50 seeds sown for these calculations. Survival in the soil seed bank was calculated by carrying out identical sowing experiments at the same site in consecutive years, recording germination in each sowing plot over several years, and assuming that germination probabilities were similar for different seed-sowing cohorts (K. Lehtilä, M. B. Garcia & J. Ehrlén, unpublished data). For example, if in year $t$ four new seedlings appeared in a plot sown with 50 seeds in $t-2$, whereas 20% of seeds sown in other plots at the same site in $t-1$ emerged as seedlings, then we assumed that 20 seeds (20 seeds × 20% seedling emergence probability = four seedlings) had been present in $t-1$, and hence that survival in the seed bank from $t-2$ to $t-1$ was 20/50 = 40%. Transitions from flowering to seeds and seedlings were calculated as the product of the average seed production of flowering individuals and the probabilities of seeds entering the seed bank and emerging as seedlings, respectively.

To increase sample sizes for matrix simulations, data for the six sites and the two transition intervals were pooled. Hence, one transition matrix was calculated for each of four treatments, based on recordings of tagged established individuals at six sites during 2 years (Table 1). In some cases matrix columns summed to more than unity. This was because a few large vegetative and reproductive rosettes split into two rosettes during the transition interval. Population density may

**Table 1.** Transition probabilities of *Primula veris* individuals, belonging to four different treatment categories, during the interval year $t$ (columns) to year $t+1$ (rows). Individuals were classified according their stage in year $t$. Stage was categorized as: seed, seedling, small, intermediate, vegetative large or flowering. Transition probabilities are pooled values for two transition intervals (1996–97 and 1997–98) and calculated as the proportion of all individuals from both censuses of stage $j$ that make the transition to stage $i$

| | Seed | Seedling | Small | Intermediate | Large | Flowering |
|---|---|---|---|---|---|---|
| Control | | | | | | |
| Seed | 0·1010 | 0 | 0 | 0 | 0 | 10·947 |
| Seedling | 0·1345 | 0 | 0 | 0 | 0 | 14·577 |
| Small | 0 | 0·5862 | 0·6667 | 0 | 0 | 0 |
| Intermediate | 0 | 0 | 0·0370 | 0·5200 | 0·0250 | 0·0101 |
| Large | 0 | 0 | 0 | 0·2800 | 0·5333 | 0·5657 |
| Flowering | 0 | 0 | 0 | 0·0400 | 0·4083 | 0·4444 |
| Vegetation removal | | | | | | |
| Seed | 0·1630 | 0 | 0 | 0 | 0 | 16·877 |
| Seedling | 0·2165 | 0 | 0 | 0 | 0 | 22·428 |
| Small | 0 | 0·6136 | 0·7015 | 0·1304 | 0 | 0 |
| Intermediate | 0 | 0 | 0·0149 | 0·6957 | 0·0685 | 0·0208 |
| Large | 0 | 0 | 0 | 0.1739 | 0·4521 | 0·4271 |
| Flowering | 0 | 0 | 0 | 0 | 0·4795 | 0·5625 |
| Litter removal plus vegetation removal | | | | | | |
| Seed | 0·1660 | 0 | 0 | 0 | 0 | 21·211 |
| Seedling | 0·2210 | 0 | 0 | 0 | 0 | 28·242 |
| Small | 0 | 0·6667 | 0·5909 | 0·0541 | 0 | 0 |
| Intermediate | 0 | 0 | 0·2727 | 0·7027 | 0·0886 | 0·0093 |
| Large | 0 | 0 | 0 | 0·1351 | 0·4810 | 0·3178 |
| Flowering | 0 | 0 | 0 | 0·0541 | 0·4177 | 0·7009 |
| Soil disturbance plus vegetation removal | | | | | | |
| Seed | 0·2705 | 0 | 0 | 0 | 0 | 21·925 |
| Seedling | 0·3605 | 0 | 0 | 0 | 0 | 29·221 |
| Small | 0 | 0·5000 | 0·3750 | 0·0217 | 0 | 0 |
| Intermediate | 0 | 0 | 0·4167 | 0·5217 | 0·0877 | 0·0444 |
| Large | 0 | 0 | 0 | 0·3696 | 0·4386 | 0·4111 |
| Flowering | 0 | 0 | 0 | 0·0652 | 0·5439 | 0·5889 |

affect transition rates of individuals (Alvarez-Buylla 1994; Freckleton *et al*. 2003). The study populations had very low densities compared with sites with an optimal management, and our primary interest was the relative performance of different treatment groups at existing densities, not in the actual population development over longer periods of time. We therefore used density-independent models and estimated the total effect of treatment on λ as the difference between transition matrices based on individuals in control plots and those based on individuals exposed to a treatment. Matrices were bootstrapped by resampling the fates of individuals and recalculating new matrices. Median values and bias-corrected 95% confidence intervals for λ were calculated from 10 000 bootstrap estimates (Caswell 2001). We used randomization tests (Levin *et al*. 1996) to assess the significance of difference in λ between treatments. To account for multiple testing, we Bonferroni-adjusted the α-level (α = 0·05/6 = 0·0083).

The total effects on population growth rate caused by treatments were decomposed into contributions from the changes induced in each of the life-cycle transitions by life table response experiment (LTRE) analysis (Horvitz, Schemske & Caswell 1997; Caswell 2001). We used a one-way fixed design in which the contributions through transitions $a_{ij}$ sums to the total treatment effect on population growth rate λ according to:

$$\partial\lambda = \sum_{i,j} (a_{ij}^{(t)} - a_{ij}^{(c)}) \times (\partial\lambda/\partial a_{ij}) \qquad \text{eqn 1}$$

where $c$ denotes the control treatment, $t$ the experimental treatment, and sensitivity $(\partial\lambda/\partial a_{ij})$ is evaluated at a matrix that is midway between the two matrices being compared (Caswell 2001). The result gives the influence of treatments on λ through effects on each respective transition in the life cycle. To calculate bias-corrected confidence intervals for the LTRE effects we bootstrapped the two matrices being compared 10 000 times, and calculated the effects for each pair of matrices (Levin *et al*. 1996).

Finally, to examine further how changes in life-cycle transitions were related to their effect on population growth rate, the size of differences in transition rates was correlated with the elasticity value of that transition in the control treatment. Elasticities $e_{ij}$ measure the proportional changes in λ resulting from a proportional infinitesimal change in matrix transition $a_{ij}$ (de Kroon *et al*. 1986; de Kroon, van Groenendael & Ehrlén 2000):

$$e_{ij} = \partial(\log\lambda)/\partial(\log a_{ij}) = (a_{ij}/\lambda)(\partial\lambda/\partial a_{ij}) \qquad \text{eqn 2}$$

Elasticities can be interpreted as the relative contribution of a transition to λ and are used to pinpoint those parts of an organism's life history that contribute most to fitness. Differences in transition rates between individuals in control and experimentally treated plots were calculated as absolute value ($a_{ij}$ of control – $a_{ij}$ of treatment)/mean $a_{ij}$.

## Results

### FITNESS COMPONENTS

Average survival over the study period did not differ between treatments or sites but was positively correlated with the average initial size (Table 2). The number of leaves per individual differed between sites but not between treatments or years. The length of the largest leaf was significantly influenced by treatments. On average, established individuals in litter removal plus vegetation removal plots and in soil disturbance plus vegetation removal plots had significantly smaller leaves than individuals in control plots ($P < 0{\cdot}03$ in both cases, for all other contrasts $P > 0{\cdot}1$, Bonferroni-adjusted pairwise tests of mean differences). In contrast, juvenile plants, i.e. belonging to the smallest non-seedling category in 1996, were twice as large in soil disturbance plus vegetation removal plots as in the other treatment plots (treatment $F_{3,7} = 16{\cdot}13$, $P = 0{\cdot}002$; site $F_{4,7} = 6{\cdot}98$,

**Table 2.** Summary test statistics of the effects of treatment on survival (1996–98), leaf number, length of largest leaf, probability of flowering, flower number in flowering individuals, leaf damage by herbivores, fruit set and capsule predation in *Primula veris*. The main factor treatment had four levels: control, vegetation removal, litter removal plus vegetation removal, and soil disturbance plus vegetation removal. Values are averages of all plants within one plot. Differences in survival were examined by two-way ANCOVA. Differences in leaf number, size of the largest leaf, probability of flowering, flower number and leaf damage was examined by repeated measurements ANCOVA. Differences in fruit set and capsule predation were examined by repeated-measurements ANOVA. For analysis of survival, average initial size was used as the covariate. For all other analyses the initial, pre-treatment, level of the response variable was used as the covariate. Presented values are test statistics and probability values for examined predictors

| Effect | Survival | Leaf number | Leaf length | Probability of flowering | Flower number | Leaf damage | Fruit set | Capsule predation |
|---|---|---|---|---|---|---|---|---|
| Treatment | $F_{3,14} = 1{\cdot}04$ | $F_{3,14} = 0{\cdot}70$ | $F_{3,14} = 6{\cdot}64$** | $F_{3,14} = 0{\cdot}20$ | $F_{3,14} = 0{\cdot}63$ | $F_{3,14} = 0{\cdot}45$ | $F_{3,11} = 0{\cdot}18$ | $F_{3,11} = 0{\cdot}50$ |
| Site | $F_{5,14} = 2{\cdot}32$ | $F_{5,14} = 5{\cdot}08$** | $F_{5,14} = 7{\cdot}07$** | $F_{5,11} = 8{\cdot}30$** | $F_{5,14} = 5{\cdot}62$** | $F_{5,14} = 28{\cdot}43$*** | $F_{5,14} = 0{\cdot}73$ | $F_{5,11} = 1{\cdot}36$ |
| Covariate | $F_{1,14} = 16{\cdot}42$*** | $F_{1,14} = 1{\cdot}86$ | $F_{1,14} = 1{\cdot}86$** | $F_{1,14} = 0{\cdot}38$ | $F_{1,14} = 7{\cdot}28$* | $F_{1,14} = 0{\cdot}26$ | | |
| Time | | $F_{1,14} = 0{\cdot}02$ | $F_{1,14} = 0{\cdot}59$ | $F_{1,14} = 0{\cdot}14$ | $F_{1,14} = 0{\cdot}12$ | $F_{1,14} = 9{\cdot}42$** | $F_{1,22} = 7{\cdot}78$** | $F_{1,22} = 8{\cdot}39$** |
| Treatment × time | | $F_{3,14} = 1{\cdot}58$ | $F_{3,14} = 0{\cdot}30$ | $F_{3,14} = 1{\cdot}94$ | $F_{3,14} = 0{\cdot}70$ | $F_{3,14} = 0{\cdot}27$ | $F_{3,22} = 0{\cdot}95$ | $F_{3,22} = 1{\cdot}94$ |
| Site × time | | $F_{5,14} = 1{\cdot}06$ | $F_{5,14} = 3{\cdot}14$* | $F_{5,14} = 0{\cdot}55$ | $F_{5,14} = 0{\cdot}77$ | $F_{5,14} = 1{\cdot}74$ | $F_{5,22} = 3{\cdot}53$** | $F_{5,22} = 11{\cdot}63$*** |
| Initial level × time | | $F_{1,14} = 0{\cdot}00$ | $F_{1,14} = 1{\cdot}86$ | $F_{1,14} = 0{\cdot}50$ | $F_{1,14} = 0{\cdot}04$ | $F_{1,14} = 0{\cdot}06$ | | |

*$P < 0{\cdot}05$, **$P < 0{\cdot}01$, ***$P < 0{\cdot}001$.

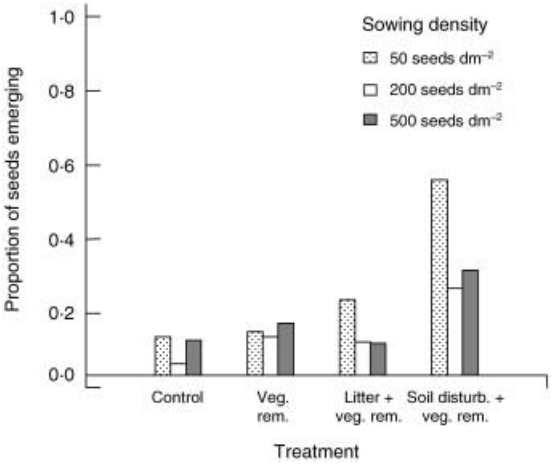


**Fig. 1.** Proportion of *Primula veris* seeds emerging as seedlings the first year after sowing for three different sowing densities and four different treatments (treatment $F_{3,60} = 11{\cdot}97$, $P < 0{\cdot}001$; sowing density $F_{2,60} = 3{\cdot}32$, $P = 0{\cdot}043$; treatment × sowing density $F_{6,60} = 0{\cdot}84$, $P = 0{\cdot}543$). Veg. rem., vegetation removal; Litter + veg. rem., litter removal plus vegetation removal; Soil disturb. + veg. rem., soil disturbance plus vegetation removal.

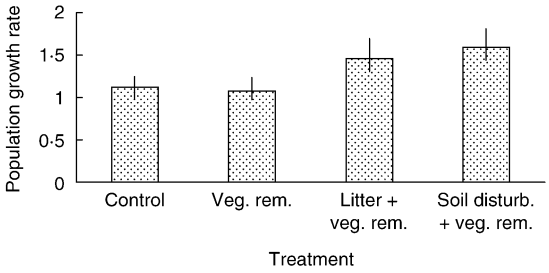


**Fig. 2.** Population growth rate of groups of *Primula veris* individuals exposed to different experimental treatments. The values presented are medians and lines denote bias-corrected 95% confidence intervals of bootstrapped values. Population growth rates of litter removal plus vegetation removal and soil disturbance plus vegetation removal treatments were both significantly higher than values of controls and vegetation removal treatments ($P < 0{\cdot}003$ for all four contrasts, randomization tests). Differences between vegetation removal and control treatments and between litter removal plus vegetation removal and soil disturbance plus vegetation removal were not significant ($P = 0{\cdot}854$ and $P = 0{\cdot}379$, respectively). Veg. rem., vegetation removal ; Litter + veg. rem., litter removal plus vegetation removal; Soil disturb. + veg. rem., soil disturbance plus vegetation removal.

$P = 0{\cdot}014$; two-way ANOVA of plot means, soil disturbance plus vegetation removal vs. other treatments $P < 0{\cdot}01$ for all three comparisons, all other contrasts $P > 0{\cdot}1$, Bonferroni-adjusted pairwise tests of mean differences). After 2 years juvenile plants in the soil disturbance plus vegetation removal treatment were three times as large as juvenile plants exposed to other treatments. The proportion of individuals that flowered and the number of flowers in flowering individuals differed between sites but there was no effect of treatment (Table 2). Fruit set was affected by year and the interaction year × site but not by treatment. Animal damage, in terms of seed predation and leaf herbivory, was not influenced by the treatments but differed between years.

Seed sowings increased average seedling number, from 0·8 in control plots to 75·2 in plots where 500 seeds were sown (sowing density $F_{3,92} = 16{\cdot}60$, $P < 0{\cdot}001$). The proportion of seeds emerging as seedlings the first year after sowing was significantly higher at low sowing densities and after soil disturbance plus vegetation removal treatments (Fig. 1). Although a smaller proportion of seeds emerged at high sowing densities, the number of seedlings was still higher. Also, the second year after sowing seedling number was higher in disturbance plots and in plots with higher sowing densities (treatment $F_{3,60} = 5{\cdot}11$, $P = 0{\cdot}003$; sowing density $F_{2,60} = 15{\cdot}64$, $P < 0{\cdot}001$; treatment × sowing density $F_{6,60} = 1{\cdot}12$, $P = 0{\cdot}359$). The size of seedlings in their second year was not affected by sowing density or treatment (treatment $F_{3,58} = 0{\cdot}71$, $P = 0{\cdot}550$; sowing density $F_{2,58} = 0{\cdot}41$, $P = 0{\cdot}666$; treatment × sowing density $F_{6,58} = 0{\cdot}99$, $P = 0{\cdot}435$). In the second sowing experiment in 1997, seedling emergence rates the first year after sowing were again significantly higher in soil disturbance plus vegetation removal plots than in control plots (treatment $F_{3,44} = 4{\cdot}60$, $P = 0{\cdot}007$; one-way ANOVA, control vs. soil disturbance plus vegetation removal $P < 0{\cdot}01$, all other contrasts $P > 0{\cdot}1$, Bonferroni-adjusted pairwise tests of mean differences).

## EFFECTS ON POPULATION GROWTH RATE

There was no effect of vegetation removal only on λ (Fig. 2). In contrast, litter removal plus vegetation removal increased λ by 0·35 compared with controls, to 1·46. The increase after soil disturbance plus vegetation removal was even larger at 0·49, and resulted in a λ-value of 1·60. The increase in λ for the litter removal plus vegetation removal treatment compared with the controls was mainly because of a higher probability that small individuals would reach an intermediate size (Fig. 3a). The second and third most important life-cycle transitions were the increased production of seedlings and the increased probability that flowering individuals would flower again the next year. Other transitions had small or non-significant effects. A higher probability that small individuals would reach an intermediate size was also the most important contribution to the difference in λ between the soil disturbance plus vegetation removal treatment and control (Fig. 3b). The second most important life cycle transition was an increased production of seedlings in disturbed plots. Differences in the other stages contributed little to differences in population growth rate.

The control and vegetation removal treatments had similar elasticity matrices (Table 3). Elasticities were highest for stasis of small and intermediate individuals, and for transitions involving large vegetative and flowering individuals (Fig. 3c and Table 3). The litter removal plus vegetation removal and soil disturbance plus vegetation removal treatments differed from the

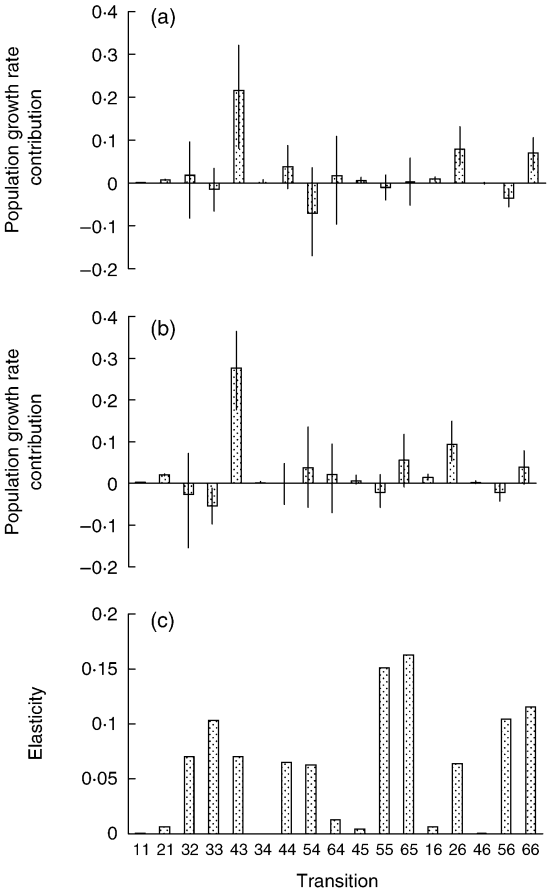


**Fig. 3.** Contributions to differences in population growth rate and elasticities for 17 different life-cycle transitions in *Primula veris*. Transitions are denoted by two-digit codes where the first digit corresponds to the stage in year $t + 1$ and the second digit to the stage in year $t$. The stages are: 1, seeds; 2, seedlings; 3, small; 4, intermediate; 5, large; 6, reproductive individuals. Contributions to differences in population growth rate were calculated by life table response experiment (LTRE) analysis (a) for control vs. litter removal plus vegetation removal treatment, and (b) for control vs. soil disturbance plus vegetation removal treatment. The values presented are medians and lines denote bias-corrected 95% confidence intervals of bootstrapped values. (c) Elasticities were calculated for individuals in the control treatment.

control in that production of seedlings, seedling survival and growth to a larger size class also had high elasticities (Table 3).

The larger the contribution of a given life cycle transition to population growth rate in terms of its elasticity, the less the proportional change in the transition rate caused by treatments (Fig. 3a–c). Negative correlations were significant for the control vs. soil disturbance plus vegetation removal ($r = -0{\cdot}468$, $n = 17$, $P = 0{\cdot}015$) but not the control vs. litter removal plus vegetation removal ($r = -0{\cdot}403$, $n = 17$, $P = 0{\cdot}109$) comparisons.

## Discussion

In this study we experimentally manipulated three components of the environment that are associated with grazing: competition for light, litter accumulation and disturbance of the topsoil layer. Fitness components of established individuals were in most cases not significantly affected by experimental treatments, whereas the responses of recruitment, juvenile growth and population growth rate were large and significant. Vegetation removal had no effect on *P. veris* but, in combination with litter removal, the effect on population performance was large, and with disturbance and complete removal of the surrounding vegetation, the effect was even stronger.

### EFFECTS OF TREATMENTS ON DIFFERENT FITNESS COMPONENTS

In established plants, survival, probability of flowering, flower number and the proportion of flowers that produced capsules were independent of treatments. An effect on probability of flowering was absent, although many plants switch from flowering to vegetative, and *vice versa*, between years (Table 2). Previous studies have shown that differences in capsule predation among populations are correlated with canopy cover (Leimu *et al*. 2002). However, in our experiment neither leaf herbivory nor capsule predation responded to manipulations of the field layer density. Litter removal plus vegetation removal and soil disturbance plus vegetation removal reduced leaf size in established individuals compared with the controls. In *Viola palustris*, leaf area decreased after experimental mowing (Jensen & Meyer 2001). A probable explanation for these results is that leaf area decreases in response to increased availability of light.

In contrast with the lack of effects in established plants, there were strong effects of treatments on seedling emergence and growth of small individuals. The stronger response in early phases of the life cycle probably reflects the fact that the negative effects of light competition and litter accumulation are largest during these phases. Increased seedling establishment in grasslands after litter removal or disturbance of the vegetation appears to be a general pattern (Facelli & Pickett 1991; Jakobsson & Eriksson 2000; Kupferschmid, Stampfli & Newberry 2001; Wilsey & Polley 2003). In our study, there were clear negative effects of seed density on the probability of seedling emergence. However, at all seed sowing densities seedling number was larger than in control plots, and in absolute terms the highest seed densities produced more seedlings and these differences also remained in the second year after sowing. This suggests that there is no saturation of seeds even at densities about 3000 times the normal seed rain, and that density-dependent interactions among seeds or emerging seedlings at realistic densities are not a major determinant of plant densities in *P. veris*.

### TOTAL EFFECTS

The difference in population growth rate between treatments was considerable. The results suggest that

**Table 3.** Elasticity matrices for populations of *Primula veris*, exposed to four different treatments. Stages are: seed, seedling, small, intermediate, vegetative large or flowering

| | Seed | Seedling | Small | Intermediate | Large | Flowering |
|---|---|---|---|---|---|---|
| Control | | | | | | |
| Seed | 0·0006 | 0 | 0 | 0 | 0 | 0·0063 |
| Seedling | 0·0063 | 0 | 0 | 0 | 0 | 0·0639 |
| Small | 0 | 0·0702 | 0·1030 | 0 | 0 | 0 |
| Intermediate | 0 | 0 | 0·0702 | 0·0651 | 0·0040 | 0·0010 |
| Large | 0 | 0 | 0 | 0·0627 | 0·1514 | 0·1043 |
| Flowering | 0 | 0 | 0 | 0·0126 | 0·1630 | 0·1153 |
| Vegetation removal | | | | | | |
| Seedling | 0·0015 | 0 | 0 | 0 | 0 | 0·0083 |
| Small | 0·0083 | 0 | 0 | 0 | 0 | 0·0475 |
| Intermediate | 0 | 0·0558 | 0·1008 | 0·0008 | 0 | 0 |
| Large | 0 | 0 | 0·0566 | 0·1154 | 0·0076 | 0·0021 |
| Flowering | 0 | 0 | 0 | 0·0655 | 0·1142 | 0·0971 |
| Seed | 0 | 0 | 0 | 0 | 0·1550 | 0·1635 |
| Litter removal plus vegetation removal | | | | | | |
| Seed | 0·0017 | 0 | 0 | 0 | 0 | 0·0136 |
| Seedling | 0·0136 | 0 | 0 | 0 | 0 | 0·1080 |
| Small | 0 | 0·1217 | 0·0824 | 0·0027 | 0 | 0 |
| Intermediate | 0 | 0 | 0·1244 | 0·1148 | 0·0027 | 0·0003 |
| Large | 0 | 0 | 0 | 0·0646 | 0·0434 | 0·0258 |
| Flowering | 0 | 0 | 0 | 0·0601 | 0·0877 | 0·1325 |
| Soil disturbance plus vegetation removal | | | | | | |
| Seed | 0·0045 | 0 | 0 | 0 | 0 | 0·0226 |
| Seedling | 0·0226 | 0 | 0 | 0 | 0 | 0·1121 |
| Small | 0 | 0·1346 | 0·0410 | 0·0009 | 0 | 0 |
| Intermediate | 0 | 0 | 0·1356 | 0·0678 | 0·0047 | 0·0016 |
| Large | 0 | 0 | 0 | 0·1031 | 0·0506 | 0·0325 |
| Flowering | 0 | 0 | 0 | 0·0379 | 0·1308 | 0·0970 |

litter is a key factor as the two treatments including litter removal had significantly higher growth rates than the two other treatments. Removal of the above-ground vegetation only appeared to have no effect on population performance, and vegetation removal with soil disturbance did not increase λ significantly compared with vegetation removal and litter removal. In another study we investigated the performance of 13 unmanipulated *P. veris* populations in different habitats (K. Lehtilä, R. Leimu, K. Syrjänen, M. B. Garcia & J. Ehrlén, unpublished data). Population growth rates were highest in grazed pastures and lowest in late successional habitats with a closed canopy. The results of this study suggest that litter accumulation is a major factor for the impoverished performance of *P. veris* populations after management abandonment. Studies with other species in grasslands have also documented effects of litter on population growth rate. Lennartsson & Oostermeijer (2001) assessed the effects of four different types of grassland management on the biennial *Gentianella campestris*. Summer mowing in combination with autumn grazing resulted in the highest population growth rate, because it simultaneously favoured the establishment of rosettes through lowered litter accumulation, and allowed for seed production. In another semelparous plant, *Cirsium vulgare*, winter, spring and summer grazing all increased population growth rates (Bullock, Hill & Silvertown 1994). In the perennial herb *Silene spaldingii* and in the annual grass *Andropogon brevifolius*, fires increase seedling recruitment and population growth rates by preventing litter accumulation (Canales *et al*. 1994; Lesica 1999).

The λ-values recorded for the litter removal plus vegetation removal and soil disturbance plus vegetation removal treatments are higher than in any of the populations subjected to detailed demographic studies in the area (0·88–1·28; K. Lehtilä, R. Leimu, K. Syrjänen, M. B. Garcia & J. Ehrlén, unpublished data). Hence, values for experimental treatments may be unrealistic in the sense that no real population will experience such favourable conditions. This is mainly because the experiment was designed so that *P. veris* plants experienced only the positive effects of vegetation removal and soil disturbance through a decreased interspecific competition, whereas they themselves were left intact. However, in real life all scenarios that involve grazing are likely to lead also to increased damage of *P. veris* individuals through eating, trampling and cutting. For example, in a nearby grazed population 67·3% of inflorescences were damaged in 1996 (K. Lehtilä, R. Leimu, K. Syrjänen, M. B. Garcia & J. Ehrlén, unpublished data). This inflorescence damage corresponds to a reduction in λ, with 0·17 for the litter removal plus vegetation removal treatment and 0·21 for the soil disturbance

plus vegetation removal treatment. Note that in these scenarios seed production decreased because of treatments, but small plants had better growth and higher survival in experimental than in control plots. Other negative effects of grazing animals are also likely. Nevertheless, our results show that in years with low grazing during flowering and seed maturation, plants may capitalize on favourable conditions. Such years may not be uncommon and indeed in 1997 the same grazed population suffered only a 2·7% loss of inflorescences. A mixture of relatively intense grazing creating conditions suitable for seedling establishment and growth, and more relaxed grazing allowing seed production, might thus be optimal for *P. veris*. Such mixtures could be achieved through among-year variation in grazing pressure, small-scale spatial heterogeneity in terms of more open areas and grazing refuges near thorny shrubs (in the study area primarily *Prunus spinosa* and *Rosa* spp.), or through late-summer grazing as in traditionally managed hay meadows.

The relationship between changes in fitness components and overall performance is determined by how sensitive population growth rate is to changes in respective components. In *P. veris* life-cycle transitions with the largest proportional change caused by the treatments contributed least to population growth rate in terms of their elasticity. This means that the magnitude of response to treatment was negatively correlated with the effect on population growth rate. Pfister (1998) interpreted such patterns as evidence that natural selection alters life histories to minimize stages with both high elasticity and high variation. The results of this study suggest that this holds true not only for unspecified variation between populations and years but also for the response to specific environmental factors.

In our relatively long-lived study species, reproduction and seedling recruitment were important for differences in population growth rate. The high importance of recruitment for population differences may appear at odds with some recent suggestions that, in long-lived plants, growth and survival contribute most to population growth (Silvertown *et al*. 1993; Silvertown, Franco & Menges 1996) and fitness depends most heavily on survival (Crone 2001). Also in our study, survival and growth of established individuals were high and made the largest contributions to population growth rate measured as elasticities. However, both survival and growth were relatively insensitive to treatments, and as a consequence they contributed little to overall differences in population growth rate between treatment groups. Instead, the life-cycle stages that responded most to treatments in terms of proportional change, growth of small individuals and seedling emergence, contributed most to the difference in λ between treatment categories.




### SYNTHESIS AND APPLICATIONS

In this study we combined experimental manipulations of components of the grazing effect with detailed recordings of the demographic response in all phases of the life cycle. This constitutes a powerful approach to identifying key phases of the life cycle and key components of the environment. Both these aspects are central to identifying optimal targets for management efforts. In our study, we identified seedling establishment as a key phase in the life cycle and litter accumulation as a key environmental factor. It is worth stressing that knowledge of only the performance during some phases of the life cycle or knowledge of only summary measures of population processes will provide us with little guidance. In our study, we used LTRE analysis to identify key phases in the life cycle. This method builds on two sources of knowledge: how treatments influence the performance during all phases of the life cycle, and how differences in life-cycle phases translate into effects on population growth rate. In an analogous way, the fact that our experimental design does not mimic the full complexity of effects caused by grazing is not a weakness but a major strength. The main advantage with isolating specific components of the grazing environment is that components can be examined and evaluated separately. Evaluating a current management regime that corresponds with a particular combination of environmental factors can tell us how this regime affects the viability of the target species. However, it provides no guidance regarding how the species will respond to management regimes that represent new combinations of environmental factors. To predict the net outcome of management types and land-use scenarios that have not previously been applied and evaluated, and to make population viability assessments applicable to situations and time frames that include new combinations of environmental conditions, it is necessary to understand how specific environmental factors influence target species during all phases of the life cycle.

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## References

Alvarez-Buylla, E.R. (1994) Density dependence and patch dynamics in tropical rain forests: matrix models and applications to a tree species. *American Naturalist*, **143**, 155–191.

Brussard, P.F. (1991) The role of ecology in biological conservation. *Ecological Conservation*, **1**, 6–12.

Bullock, J.M., Hill, B.C. & Silvertown, J. (1994) Demography of *Cirsium vulgare* in a grazing experiment. *Journal of Ecology*, **82**, 101–111.

Burgman, M.A., Akcakaya, H.R. & Loew, S.S. (1998) The use of extinction models for species conservation. *Biological Conservation*, **43**, 9–25.

Canales, J., Trevisan, M.C., Silva, J.F. & Caswell, H. (1994) A demographic study of an annual grass (*Andropogon brevifolius*

Schwarz) in burnt and unburnt savanna. *Acta Oecologia*, **15**, 261–273.
Caswell, H. (1989) *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer, Sunderland, MA.
Caswell, H. (2001) *Matrix Population Models*, 2nd edn. Sinauer, Sunderland, MA.
Crone, E.E. (2001) Is survivorship a better fitness surrogate than fecundity? *Evolution*, **55**, 2611–2614.
Ehrlén, J. (2003) Fitness components vs. total demographic effects: evaluating herbivore impacts on a perennial herb. *American Naturalist*, **162**, 796–810.
Facelli, J.M. & Pickett, S.T.A. (1991) Plant litter: light interception and effects on an old-field plant community. *Ecology*, **72**, 1024–1031.
Freckleton, R.P., Matos, D.M.S., Bovi, M.L.A. & Watkinson, A.R. (2003) Predicting the impacts of harvesting using structured population models: the importance of density-dependence and timing of harvest for a tropical palm tree. *Journal of Applied Ecology*, **40**, 846–858.
Horvitz, C.C. & Schemske, D.W. (1995) Spatiotemporal variation in demographic transitions of a tropical understorey herb: projection matrix analysis. *Ecological Monographs*, **65**, 155–192.
Horvitz, C.C., Schemske, D.W. & Caswell, H. (1997) The relative 'importance' of life-history stages to population growth: prospective and retrospective analyses. *Structured Population Models in Marine, Terrestrial and Freshwater Systems* (eds S. Tuljapurkar & H. Caswell), pp. 247–272. Chapman & Hall, New York, NY.
Hultén, E. (1971) *Atlas över växternas utbredning i Norden*, 2nd edn. Generalstabens litografiska anstalts förlag, Stockholm, Sweden.
Hultén, E. & Fries, M. (1986) *Atlas of North European Vascular Plants: North of the Tropic of Cancer*. Koeltz Scientific Books, Königstein, Germany.
Inghe, O. & Tamm, C.O. (1988) Survival and flowering of perennial herbs. V. Patterns of flowering. *Oikos*, **51**, 203–219.
Jakobsson, A. & Eriksson, O. (2000) A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos*, **88**, 494–502.
Jensen, K. & Meyer, C. (2001) Effects of light competition and litter on the performance of *Viola palustris* and on species composition and diversity of an abandoned fen meadow. *Plant Ecology*, **155**, 169–181.
de Kroon, H., van Groenendael, J.M. & Ehrlén, J. (2000) Elasticities: a review of methods and model limitations. *Ecology*, **81**, 607–618.
de Kroon, H., Plaisier, A., van Groenendael, J. & Caswell, H. (1986) Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology*, **67**, 1427–1431.
Kupferschmid, A.D., Stampfli, A. & Newberry, D.M. (2001) Dispersal and microsite limitation in an abandoned calcareous grassland of the southern prealps. *Folia Geobotanica*, **35**, 125–141.
Leimu, R., Syrjänen, K., Ehrlén, J. & Lehtilä, K. (2002) Pre-dispersal seed predation in *Primula veris*: among-population variation in damage intensity and selection on flower number. *Oecologia*, **133**, 510–516.
Lennartsson, T. & Oostermeijer, J.G.B. (2001) Demographic variation and population viability in *Gentianella campestris*: effects of grassland management and environmental stochasticity. *Journal of Ecology*, **89**, 451–463.
Lesica, P. (1999) Effects of fire on the demography of the endangered, geophytic herb *Silene spaldingii* (Caryophyllaceae). *American Journal of Botany*, **86**, 996–1002.
Levin, L., Caswell, H., Bridges, T., DiBacco, C., Cabrera, D. & Plaia, G. (1996) Demographic responses of estuarine polychaetes to pollutants: life table response experiments. *Ecological Applications*, **6**, 1295–1313.
Norris, K. (2004) Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. *Journal of Applied Ecology*, **41**, 413–426.
Oostermeijer, J.G.B., Brugman, M.L., de Boer, E.R. & den Nijs, H.C.M. (1996) Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. *Journal of Ecology*, **84**, 153–166.
Pfister, C.A. (1998) Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences USA*, **95**, 213–218.
Silvertown, J., Franco, M. & Menges, E. (1996) Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. *Conservation Biology*, **10**, 591–597.
Silvertown, J., Franco, M., Pisanty, I. & Mendoza, A. (1993) Comparative plant demography: relative importance of life-history components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology*, **81**, 465–476.
Tamm, C.O. (1972) Survival and flowering of some perennial herbs. III. The behaviour of *Primula veris* on permanent plots. *Oikos*, **23**, 159–166.
Thompson, K., Bakker, J.P. & Bekker, R.M. (1997) *The Soil Seed Bank of North Western Europe: Methodology, Density and Longevity*. Cambridge University Press, Cambridge, UK.
Wedderburn, F. & Richards, A.J. (1990) Variation in within-morph incompatibility inhibition sites in heteromorphic *Primula* L. *New Phytologist*, **116**, 149–162.
Wilsey, B.J. & Polley, H.W. (2003) Effects of seed additions and grazing history on diversity and productivity. *Ecology*, **84**, 920–931.

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